PAPPUS VARIATION IN NORTH AMERICAN ASTERS. I. DOUBLE, TRIPLE AND QUADRUPLE PAPPUS IN *SYMPHYOTRICHUM* AND RELATED ASTER GENERA (ASTERACEAE: ASTEREAE)

John C. Semple and Jennifer L.A. Hood

Department of Biology
University of Waterloo
Waterloo, Ontario, CANADA N2L 3G1
jcsemple@sciborg.uwaterloo.ca

ABSTRACT

The pappus traits of 84 taxa of *Canadanthus, Ampelaster, Psilactis,* and *Symphyotrichum* (subtribe Symphyotrichinae) and 14 other species of asters were examined. Most species of Symphyotrichinae had a pappus consisting of three whorls: 1) a secondary inner whorl of a few bristles 40–85% the length of the inner primary whorl, 2) a primary outer whorl of many bristles with tapering ends about 90–95% the length of the inner primary whorl, and 3) a primary inner whorl of many bristles with very weakly to strongly clavate ends. In addition, a few species of *Symphyotrichum* have a vestigial secondary outer whorl of a single short bristle only about 10–30% the length of the primary inner whorl. In some species of *Symphyotrichum* the secondary inner whorl was difficult to distinguish from the primary outer whorl or possibly was absent. In a small sample of species of *Aster, Doellingeria, Eurybia, Eucephalus, Galatella, Herrickia, Ionactis, Oclemena,* and *Oreostemma,* the pappus was either triple or quadruple. The short secondary outer whorl was present in most species examined but was sometimes reduced to very few bristles or absent on some fruits. In some cases, the secondary inner whorl of mid length tapering bristles was present in some individuals in a species but not in others. The quadruple pappus with strongly clavate inner bristles appears to be plesiomorphic for the North American Clade of the tribe Astereae. In single species samples of *Crinitaria, Linosyris,* and *Felicia* the pappus differed from that of other species examined.

RESUMEN

Se examinaron las caracteristicas de los vilanos de 84 taxa de *Canadanthus, Ampelaster, Psilactis,* y *Symphyotrichum* (subtribu Symphyotrichinae) y otras 14 especies de compuestas. La mayoria de las especies de Symphyotrichinae tienen un vilano de tres verticilos: 1) un verticilo secundario interno de pocas sedas con el 40–85% de la longitud del verticilo interno primario, 2) un verticilo externo primario con muchas sedas de extremos estrechados de aproximadamente el 90–95% de la longitud del verticilo interno primario, y 3) un verticilo interno primario de muchas sedas con extremos desde débilmente a fuertemente clavados. Además, algunas especies de *Symphyotrichum* tienen un verticilo secundario externo vestigial de una sola seda aproximadamente del 10–30% de la longitud del verticilo interno primario. En algunas especies de *Symphyotrichum* el verticilo secundario interno fue difícil de diferenciar del primario externo o posiblemente estaba ausente. En una pequeña muestra de especies de *Aster, Doellingeria, Eurybia, Eucephalus, Galatella, Herrickia, Ionactis, Oclemena,* y *Oreostemma,* el vilano era triple o cuádruple. El verticilo secundario externo corto estaba presente en la mayoría de las especies examinadas pero estaba reducido algunas veces a unas pocas sedas o ausente en algunos frutos. En algunos casos, el verticilo interno secundario de sedas de tamaño mediano estaba presente en algunos individuos de una especie pero no en otros. El vilano cuádruple con las sedas

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interiores fuertemente clavadas parece ser plesiomórfico para el clado Norte Americano de la tribu Astereae. En una sola muestra de especies de *Crinitaria*, *Linosyris*, y *Felicia* el vilano difería de las otras especies examinadas.

INTRODUCTION

The symphyotrichoid aster genera *Canadanthus* Nesom, *Ampelaster* Nesom, and *Symphyotrichum* Nees have long been reported to have a simple pappus with non-clavate bristles, either as species of *Aster* L. (e.g., Gray 1884; Fernald 1950; Cronquist 1955, 1968a, 1980, 1994) or recently as species of *Canadanthus*, *Ampelaster*, and *Symphyotrichum* (Nesom 1994, 2000; Semple et al. 2002). In contrast, some other North American asters historically treated at times in other genera or in *Aster* sensu lato have been reported to have a double (*Eucephalus* Nutt., *Sericocarpus* Nees; Gray 1884; Cronquist 1955) or a triple pappus (*Doellingeria* Nees; Cronquist 1968, 1980; Nesom 1994; Semple et al. 2002). The putatively double pappus consisted of a short whorl of outer bristles and a much longer whorl of inner bristles, while the putatively triple pappus had a short outer whorl and two long inner whorls, the outer slightly shorter and tapering and the inner bristles clavate. Species of *Solidago* L. historically were also considered to have a simple pappus (e.g., Gray 1884; Fernald 1950; Cronquist 1968b, 1980; Nesom 2000; Semple et al. 1999). However, Hood and Semple (2003) demonstrated that nearly all species of goldenrods had a double pappus with two primary whorls of long bristles (the outer shorter and tapering, the inner clavate) and at least some species had an additional secondary outer whorl of a few very short bristles. That is, a genus thought to have a simple pappus in fact had a triple pappus like that reported for *Doellingeria* (synonym: Aster sect. *Triplopappus* Torr. & A. Gray; Torrey and Gray 1841; Semple et al. 2002). Our discovery that goldenrods had a double (or rarely triple) pappus raised the possibility that other genera of Astereae thought to have a simple pappus might also be double or triple. This paper on pappus variation is one in a series being prepared by the first author's lab to report the findings of investigations of cypselae traits, including pappus variation in the North American Clade of the Asteraeae (sensu Noyes & Rieseberg 1999). The pappus whorl terminology proposed by Hood and Semple (2003; secondary outer whorl, primary outer whorl, and primary inner whorl) is used throughout this paper with the addition of new label for a fourth whorl not seen in *Solidago*, the secondary inner whorl of tapered mid length bristles.

MATERIALS AND METHODS

A preliminary survey was undertaken to examine under the dissecting microscope the pappus bristles of one or two specimens of representative species of the sections and subsections of *Symphyotrichum*. Subsequently, a more rigorous survey was conducted involving 80 taxa and one hybrid of *Symphyotrichum*

and 4 species of other genera in the subtribe Symphyotrichinae Nesom and 14 species of other North American and Eurasian aster genera listed in Table 1. Observations were made using a dissecting scope (10–70×) or a compound light microscope (20–400×). The degree of the clavateness of bristle tips was determined using the 0–4 rankings described in detail in Hood and Semple (2003). At least five different fruits from each species were observed under the dissecting microscope at a maximum of 70×; most observations were made at 30–40×. For the most part, observations were made on specimens in the WAT Herbarium, but additional material on loan from BRIT, CAN, GH, and NY (Holmgren et al. 1990) was also examined to expand the number of taxa. In addition to several methods used in evaluating pappus features listed by Hood and Semple (2003), assessment of the presence or absence of any short secondary outer whorl linear to scaly bristles and other pappus features were also systematically undertaken. Thus, Table 1 has five columns of observational data plus a column for additional comments, while only four columns were included by Hood and Semple (2003).

Observations on the compound microscope were made from slides prepared as follows. For each species, two ray floret and two disc floret cypselae (with corollas or without corollas still attached) were mounted in Cytoseal^{TM} 60 (low viscosity) mounting medium under a cover slip. Observations at 100–400× on the compound microscope were made similarly to the observations under the dissecting scope at 30–70×. Observations made on the two kinds of scopes were compared and any discrepancies were resolved by re-examining specimens.

Digital photomicrographs were taken using a Nikon CoolPix 990 camera manually held against the ocular lens of either the dissecting or compound microscope. Pictures were taken of specimens under the compound light microscope with either below stage or above stage lighting. Final digital illustrations were made using CorelDraw 12® from digital images edited with Corel PhotoPaint12® (Corel Corp.).

RESULTS AND DISCUSSION

The pappus of the majority of species of the Symphyotrichinae consists of three whorls (Figs. 1–4): 1) a secondary inner whorl of a few intermediate length, fine, tapering bristles usually about 50–70% of the length of the primary inner whorl, 2) a primary outer whorl of tapering, non-clavate bristles that were generally 5–10% shorter than the inner whorl, and 3) a primary inner whorl of very weakly to strongly clavate tipped bristles. The phylogenetically more basal taxa of the Symphyotrichinae *Canadanthus modestus* (Lindl.) Nesom (Figs. 1A–G), *Ampelaster carolinanus* (Walt.) Nesom (Figs. 1H–K), and *Almutaster pauciflorus* (Nutt.) Löve & Löve (Figs. 2A–E) are all diploids ($2n = 18$) with $x = 9$ chromosomal base number (Brouillet et al. 2001a, b; Semple et al. 2002). These have a triple pappus with no secondary outer whorl of short bristles or scales observed.

TABLE 1. Pappus variation in subtribe Symphyotrichinae: *Symphyotrichum* and related genera. **Clv**, degree of clavateness of inner bristles (0 = not clavate to 4 = strongly clavate); **Clv-Tap**, clavate alternating with tapered bristles (primary inner and outer whorls, y = yes, – not obviously so); **Lgth**, primary outer bristles shorter than primary inner bristles; **Ovrlp**, degree of overlapping of bristles at base (0= not observed; 1=slight overlap; 2= definite overlap); **2nd-Out**, evidence for a secondary outer whorl of very short scaly-bristles.

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
SYMPHYOTRICHINAE Nesom						
Canadanthus Nesom (*x* = 9)						
C. modestus	1	y	y	2	n	2nd inner bristles 60% of 1° inner
Ampelaster Nesom (*x* = 9)						
A. carolinianus	2	y	y	0	n	2nd inner, few, 50% of 1° inner
Almutaster Löve (*x* = 9)						
A. pauciflorus	1	y	y	0	n	2nd inner 50–60% of 1° inner
Psilactis A. Gray (*x* = 9, 4, 3)						
P. tenuis (*x* = 4)	1	y	y	0	n	heterocarpic, ray fruit epappose; 2nd inner bristle 40–60% of 1° inner
Symphyotrichum Nees						
subg. ***Chapmaniani*** (Semple) Semple (*x* = 7)						
S. chapmanii	2	y	y	2	y	2nd inner, few, 50–60% of 1° inner; possible 2nd outer whorl bristle, one seen, fine, 30% of 1° inner
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Symphyotrichum* series *Symphyotrichum*						
S. novi-belgii	0	–	y	0	n	2nd inner, very few, 70% of 1° inner
S. retroflexum	4	y	y	2	y	2nd inner bristles, few , 70–8% of 1° inner; possible 2nd outer bristle, 30% of 1° inner, only seen on one fruit
S. robynsianum	0	–	y	0	n	2nd inner, few, 70–80% of 1° inner
series *Punicei* (House) Semple						
S. elliottii	2	y	y	1	n	2nd inner, few, 70–80% of 1° inner

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
S. prenanthoides	0	–	y	0	n	2nd inner, few, 60–80% of 1° inner
S. puniceum	0	–	y	2	n	2nd inner bristles, few, 40–70% of 1°
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Occidentales* (Rydb.) Nesom (*Foliacei*)						
S. chilense	3	y	y	1	n	2nd inner, few, 75–80% of 1° inner
S. eatonii	2	y	y	0	n	2nd inner, few, 75–80% of 1° inner
S. foliaceum	3	y	y	0	n	2nd inner, very few, 80% of 1° inner
S. jessicae	2	y	y	0	n	2nd inner, very few, 70–80% of 1°
S. spathulatum	3	y	y	0	n	2nd inner, very few, 70–80% of 1°
S. subspicatum	3	y	y	0	n	2nd inner bristles not seen
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Heterophylli* (Nees) Semple series *Cordifolii* (G. Don in Loudon) Semple						
S. anomalum	1	y	y	1	n	2nd inner bristles, few, 80% of 1°
S. ciliolatum	0	y	y	0	n	2nd inner bristles, few, 70–80% of 1°
S. cordifolium	1	y	y	0	n	2nd inner bristles, few, 70% of 1°
S. drummondii	1	y	y	0	n	2nd inner bristles, few, 70% of 1°
S. shortii	1	y	y	1	n	2nd inner bristles, few, 70% of 1°
S. texanum	1	y	y	0	n	2nd inner bristles, few, 70–80% of 1°
S. undulatum	2	y	y	0	n	2nd inner bristles, few, 80% of 1°
S. urophyllum	0	y	y	0	n	variable bristle lengths; 2nd inner bristles, few, 60–70% of 1°; 1° outer 85–90% of 1° inner series *Concinni* (Nees) Semple
S. laeve	2	y	y	0	n	2nd inner bristles, few, 70–80% of 1°
S. oolentangiense	3	y	y	2	n	2nd inner bristles, few, 70–80% of 1°
S. attenuatum	0	–	y	0	n	2nd inner bristles 60–70% of inner
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Dumosi* (Torr. & A. Gray) Nesom						
S. boreale	0	–	y	0	n	2nd inner bristles, few, 60–70% of 1°
S. dumosum						
var. *dumosum*	1	y	y	0	n	2nd inner, 0–few, 70–80% of 1° inner
var. *strictior*	2	y	y	0	n	2nd inner, very few, 70% of 1° inner

TABLE 1. (continued)

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Dumosi* (Torr. & A. Gray) Nesom (continued)						
S. eulae	3	y	y	0	n	2nd inner bristles not seen
S. lanceolatum						
subsp. *hesperium*	1	y	y	0	y	2nd inner bristles, few, 50–60% of 1°; 2nd out bristle, one seen, 10% of 1° subsp. *lanceolatum*
var. *hirsuticaule*	1	y	y	0	n	2nd inner bristles, few, 70 of 1°
var. *interior*	2	y	y	1	n	2nd inner bristles, few, 70% of 1°
var. *lanceolatum*	2	y	y	1	n	2nd inner bristles, few, 80% of 1°
var. *latifolium*	2	y	y	0	n	2nd inner bristles, few, 80% of 1°
S. lateriflorum						
var. *lateriflorum*	2	y	y	0	n	2nd inner bristles, few, 80% of 1°
var. *angustiflolium*	1	y	y	0	n	2nd inner bristles, few, 80% of 1°
S. nahanniense	1	y	y	1	n	2nd inner bristles 50–70% of 1° inner
S. praealtum						
var. *angustior*	2	y	y	2	n	2nd inner bristles, very few, 70–80% of 1° inner
var. *praealtum*	2	y	y	0	n	2nd inner bristles, few, 80% of 1°
S. ontarione						
var. *ontarione*	2	y	y	1	n	2nd inner bristles, few, 40–80% of 1°
S. racemosum	1	y	y	0	n	2nd inner bristles not seen; small fruit
S. simmondsii	1	y	y	1	n	2nd inner bristles, few, 70% of 1°
S. tradescanti	1	y	y	0	n	2nd inner bristles, few, 80% of 1°
S. welshii	1	y	y	1	n	2nd inner bristles 50–70% of 1° inner
subg. ***Symphyotrichum*** sect. *Symphyotrichum* (*x* = 8) subsect. *Porteriani* (Rydb.) Nesom						
S. depauperatum	0	–	y	0	n	2nd inner bristles, 0–few, 80% of 1°
S. parviceps	0	–	y	0	n	2nd inner bristles, few, 60–70% of 1°
S. porteri	2	y	y	0	n	2nd inner, 0–few, 60–70 % of 1° inner

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
S. pilosum						
var. *pilosum*	2	y	y	1	n	2nd inner, 0–few, 50–60% of 1°
var. *pringlei*	2	y	y	0	n	2nd inner bristles, 0–few, 80% of 1°
S. priceae	2	y	y	0	n	2nd inner, very few, 80% of 1° inner
sect. Conyzopsis (Torr. & Gray) Nesom ($x = 7$)						
S. frondosum	0	–	y	0	n	2nd inner not obvious; 1° bristles fine and of slightly different lengths
S. ciliatum	0	–	y	0	n	2nd inner not obvious; 1° bristles fine and of slightly different lengths
S. laurentianum	1	y	y	0	n	2nd inner not obvious; 1° bristles fine and of slightly different lengths
sect. *Turbinelli* (Rydb.) Semple ($x = 48$ derived from $x=8$)						
S. turbinellum	1	y	y	0	n	2nd inner, 1–few, 70–80% of 1° inner
subg. ***Ascendentes*** (Rydb.) Semple ($x = 13, 21$)						
S. ascendens	3	y	y	0	n	2nd inner bristles, few, 60–70% of 1°
S. defoliatum	1	y	y	0	n	2nd inner, very few, 80% of 1° inner
subg. ***Virgulus*** (Raf.) Nesom ($x = 5, 4$) sect. *Concolores* (Torr. & A. Gray) Nesom						
S. sericeum	1	y	y	2	y	2nd inner bristles, few, 60–70% of 1° inner; 2nd outer bristle, one seen on one fruit, 25% of ° inner
S. pratense	1	y	y	2	n	2nd inner bristles 40–80% of 1° inner
S. concolor						
var. *concolor*	1	y	y	0	n	2nd inner bristles, few, 50–60% of 1°
var. *divestitum*	1	y	y	0	n	2nd inner bristles, few, 60–80% of 1°
S. plumosum	1	y	y	1	n	2nd inner bristles 50–80% of 1° inner
subg. ***Virgulus*** (Raf.) Nesom ($x = 5, 4$) sect. *Grandiflori* (Torr. & A. Gray) Nesom subsect. *Grandiflori* (Torr. & A. Gray) Nesom						
S. campestre	3	y	y	1	n	2nd inner bristles, few, 40–70% of 1°
S. fendleri	2	y–	y	1	n	2nd inner bristles, few, 50–60% of 1°

TABLE 1. (continued)

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
subsect. *Grandiflori* (Torr. & A. Gray) Nesom (continued)						
S. grandiflorum	2	y	y	1	n	2nd inner bristles, few, 60–70% of 1°
S. oblongifolium	2	y	y	0	n	2nd inner bristles, few, 60–80% of 1°
S. yukonense	2	y	y	1	y	single short 2nd outer bristle seen; 2nd inner bristles 40–60%, fine; lower barbs of 1° bristles anthocyanotic
subsect. Mexicanae Nesom						
S. moranense	3	y	y	2	n	2nd inner bristles, few, 50–70% of 1°
S. trilineatum	2	y	y	2	n	2nd inner bristles, few, 60–70% of 1°
subg. ***Virgulus*** (Raf.) Nesom (*x* = 5, 4) sect. *Patentes* (Torr. & A. Gray) Nesom						
subsect. Patentes (Torr. & A. Gray) Nesom						
S. patens						
var. *patens*	3	y	y	1	n	2nd inner bristles, few, 60–80% of 1°
var. *patentissimum*	3	y	y	2	n	2nd inner bristles, few, 70–80% of 1°
S. phlogifolium	1	y	y	1	n	2nd inner bristles, few, 50–70% of 1°
S. georgianum	3	y	y	2	n	2nd inner bristles, few , 70% of 1°
subsect. *Brachyphylli* (Torr. & A. Gray) Nesom						
S. adnatum	2	y	y	0	n	2nd inner bristles, few, 50–70% of 1°
S. walteri	1	y	y	1	n	2nd inner bristles, few, 50–80% of 1°
subg. ***Virgulus*** (Raf.) Nesom (*x* = 5, 4) sect. *Polyliguli* (Semple & Brouillet) Semple						
S. novae-angliae	0	–	y	2	n	2nd inner bristles, few ,50–70% of 1°
S. ×amethystinum	0	–	y	0	n	2nd inner bristles, few, 50–80% of 1°
subg. ***Virgulus*** (Raf.) Nesom (*x* = 5, 4) sect. *Ericoidei* (Torr. & A. Gray) Nesom						
S. ericoides						
subsp. *ericoides*	2	y	y	1	n	2nd inner bristles, few, 70–80% of 1°
subsp. *pansum*	1	y	y	1	n	2nd inner bristles, few, 70–80% of 1°
S. falcatum	2	y	y	0	n	2nd inner bristles, few, 70–80% of 1°

TABLE 1. (continued)

Taxon	CIv	CIv-Tap	Lgth	Ovrlp	2nd-Out	Comments
subg. **Astropolium** (Nutt.) Semple ($x = 5$)						
S. subulatum var. *subulatum*	0	y	y	0	n	not clearly in three whorls; 2nd inner bristles, very few, 70–80% of 1°
S. tenuifolium var. *tenuifolium*	1	y	y	0	n	2nd inner bristles nearly as long as 1° outer bristles, or not present
EXAMPLES OF OTHER ASTER GENERA OF THE NORTH AMERICAN CLADE						
Doellingeria umbellata var. *umbellata*	3	y	y	2	y	2nd outer bristles, many, 10–15% of 1° inner bristles
Eucephalus engelmannii	4	y	y	2	y	2nd outer bristles, few, linear, 10–20% of 1° inner bristles; some individuals have a 2nd inner whorl of bristles 35–75% of 1° inner whorl
Eurybia macrophylla	3	y	y	2	y	2nd outer bristles, very few, 10–15% of inner bristles; some individuals have a 2nd inner whorl of bristles 50–60% of 1° inner whorl
Herrickia glauca	2	y	y	2	y	2nd outer bristles, very few 10–25%; 2nd inner bristles, few, 50–80% of 1° inner
Ionactis linariifolia	3	y	y	2	y	2nd outer bristles, many, 10–20% of 1° inner bristles; some individuals have a 2nd inner whorl of bristles 35–75% of 1° inner bristles
Oclemena reticulata	3	y	y	2	y	2nd outer bristles, few, 10–20% of inner bristles; 2nd inner bristles few, 40–60% of 1° inner

TABLE 1. (continued)

Taxon	Clv	Clv-Tap	Lgth	Ovrlp	2nd-Out	Comments
EXAMPLES OF OTHER ASTER GENERA OF THE NORTH AMERICAN CLADE (continued)						
Oreostemma alpigenus ssp. *haydeni*	3	y	y	2	y	2^{+0} outer bristles, few, 10–15% of inner bristles; 2^{+1} inner bristles 40–60% of 1° inner bristles
EXAMPLES OF BASAL GRADE ASTERS						
Aster amellus	2	y	y	2	y	2^{+1} outer bristles very few, 10–30% of 1° inner; 2^{+1} inner bristles few,50–80% of 1° inner
Aster ageratoides subsp. *leiophyllus*	1–2	y	y	2	y	2^{+0} outer bristles very few, 20–25% of 1° inner; 2^{+1} inner bristles few, 50–60% of 1° inner
Aster scaber	3	y	y	2	y	2^{+1} outer bristles, few, 15–35% of 1° inner; 2^{+1} inner bristles, few, 40–70% of 1° inner
Galatella punctata	2	y	y	2	y	2^{+1} outer bristles very few; ca. 30% of 1° inner; 2^{+1} inner bristles few, 50–60% of 1° inner
Crinitaria linosyris	1	y	y	2	y	whorls grade outer to inner and not clearly discontinuous; 2^{+1} outer bristles very few, 30–40% of 1° inner; 2^{+1} inner bristles, 50–60% of 1° inner
Linosyris villosa	1?	?	?	2	y	numerous bristle, 70 plus; whorls grade outer to inner, shortest outer bristles 15% the length of the longest inner; inner most bristles only weakly clavate
Felicia amelloides	0–1	?	?	0	n	possibly two whorls, some bristles narrowly clavate, some variation in length, no short to mid length bristles

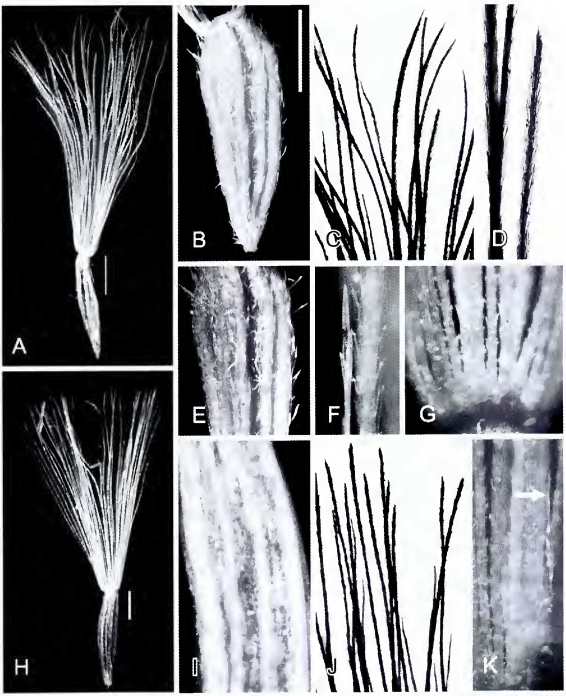

FIG. 1. Cypselae traits in *Canadanthus* and *Ampelaster*, disc fruits; scale bars = 1 mm. **A–G.** *Canadanthus modestus* (*Semple & Brouillet 7008* WAT). **A.** Immature fruit. **B.** Fruit body. **C.** Silhouette of tips of primary outer bristles (short, tapering) and primary inner bristles (longer, clavate). **D.** Clavate tip of primary inner whorl bristle. **E.** Mature fruit body detail. **F.** Tip of primary outer whorl bristle. **G.** Base of primary pappus whorls. **H–K.** *Ampelaster carolinianus* (*Semple 5393* WAT). **H.** Mature fruit. **I.** Detail of cypsela body. **J.** Silhouette of tips of primary outer bristles (short, tapering) and primary inner bristles (longer, clavate). **K.** Base of primary pappus whorls and single secondary pappus whorl bristle (arrow).

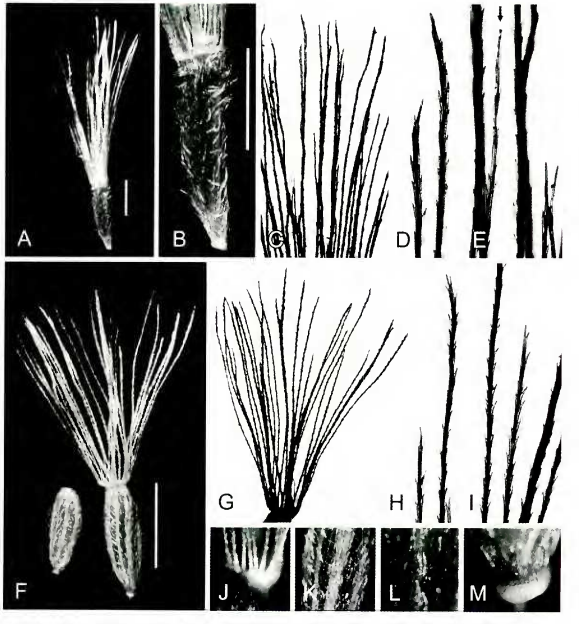

FIG. 2. Pappus traits in *Almutaster* and *Psilactis*; scale bars = 1 mm. **A–E.** Disc fruit, *Almutaster pauciflorus* (*Semple & Semple 5763* WAT). **A.** Mature fruit. **B.** Fruit body. **C.** Silhouette of pappus bristle tips. **D.** Clavate tips of primary inner whorl bristles. **E.** Tip of primary outer whorl bristle (arrow); the two shorter bristles on the right are possible long secondary outer bristles. **F–M.** *Psilactis tenuis (Semple & Heard 8201* WAT). **E.** Heterocarpic ray (epappose) and disc fruit. **G–M.** Disc fruit. **G.** Silhouette of pappus. **H.** Tips of primary whorl bristles. **I.** Tip of long secondary outer whorl bristle. **J.** Base of pappus whorls. **K.** Surface of fruit body. **L.** Detail of ridge of fruit body. **M.** Swollen base of fruit.

The much more derived, heterocarpic *Psilactis tenuis* (Figs. 2F–M) with $2n = 8$ had ray fruits without a pappus and disc fruits with what we interpret as a triple pappus. The mid length secondary inner bristles are obvious (Fig. 1G), but there was little difference in the primary outer and inner whorl bristles except length (Figs. 2G–I).

Within the large genus *Symphyotrichum*, with $x = 8, 7, 6, 5$ and 4 and diploid to duodecaploid taxa, there was some correlation between infrageneric

group and degree of clavateness, but there was also considerable variation even between closely related species within the same subsection or even series. For example in *S.* series *Symphyotrichum*, *S. retroflexum* (Lindl.) Nesom (Figs. 4A–F) with $2n = 48$ had the most strongly clavate inner bristles in the genus and a few secondary inner whorl bristles, while *S. novi-belgii* (L.) Nesom with $2n = 48$ had non-clavate inner bristles and the secondary inner bristles were difficult to detect. All members of *S.* subsect. *Occidentales* had inner primary whorl bristles with well developed clavate tips. Most members of *S.* subsect. *Heterophylli* had non-clavate to weakly clavate inner primary bristles, while in the closely related subsect. *Dumosi*, species ranged from having non-clavate to strongly clavate primary inner bristles. Secondary inner bristles were generally few in number and 70–80% the length of the primary inner bristles. In subsect. *Porteriani*, the small fruits had relatively few bristles and very few secondary inner bristles. All these taxa have $x = 8$ and are members of subg. *Symphyotrichum*. This range in variation was also present in *S.* subg. *Virgulus* with $x = 5$, but the secondary inner whorl was more easily recognized as present, more variable in length, and with more and shorter bristles (40–80%).

The most distinct pappus in *Symphyotrichum* occurred in the three members of sect. *Conyzopsis*, which have $x = 7$ (Houle & Brouillet 1985). These have been treated as members of the separate genus *Brachyactis* Ledeb. (Jones 1989) but are likely derived from, or are sister group to, the western North American $x = 8$ *Foliacei* group (subsect. Occidentales; Semple et al. 2002 and earlier cited references). Conyzopsoid asters have a pappus with numerous fine bristles that are not clavate (Figs. 4I–L). The primary outer whorl is variable in length and shorter than the primary inner bristles. We saw no clear evidence of a secondary outer whorl. In short, in addition to having a derived chromosomal base number, being taprooted annuals rather than perennials like all other species in the genus, and being in other ways atypical members of the genus, the conyzopsoid asters also have a derived pappus that is apparently reduced to double, not triple or clavate, and they are the only species within *Symphyotrichum* with accrescent bristles (Nesom 1994).

Within *Symphyotrichum* it is sometimes difficult to distinguish between the whorls of bristles. As in *Solidago* (Hood & Semple 2003), the smaller cypselae with fewer bristles show less evidence for a multiple-whorled pappus. This was more often the case in sect. *Symphyotrichum*.

While most species of *Symphyotrichum* have a triple pappus, a few species also possess a vestigial secondary outer whorl. Only one short bristle was observed on one fruit in each case. These occurred in three different subgenera: subg. *Chapmanii*, *S. chapmanii*; subg. *Symphyotrichum*, *S. lanceolatum* subsp. *hesperium* and *S. retroflexum*; and subg. *Virgulus*, *S. sericeum* and *S. yukonense* (Fig. 3M). The same situation was observed in *Solidago* (Hood & Semple 2003), although for this report greater effort was made to detect the often difficult to

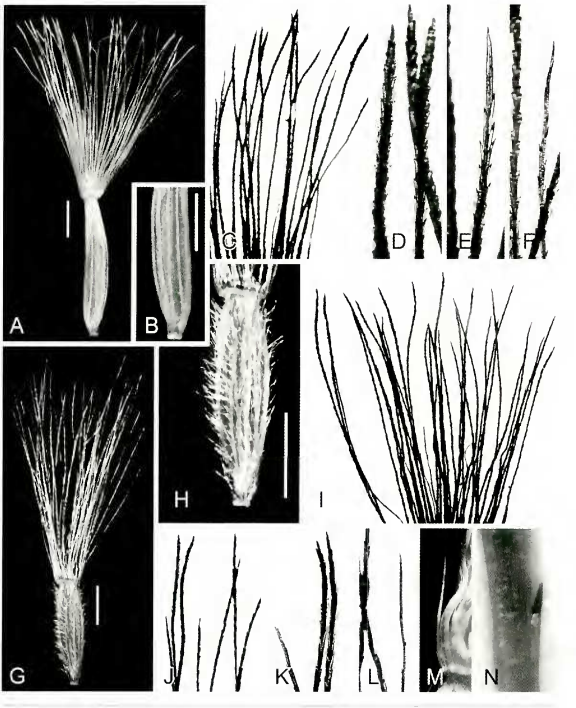

Fig. 3. Fruit traits in *Symphyotrichum*, disc fruits; scale bars = 1 mm. **A–F.** Subg. *Chapmaniani*, *S. chapmanii* (*Canne 2277* WAT). **A.** mature fruit. **B.** Fruit body detail. **C.** Silhouette of upper portion of pappus. **D.** Tips of primary inner whorl bristles. **E.** Tip of primary outer whorl bristle. **F.** Tip of secondary outer whorl bristle. **G–M.** Subg. *Virgulus*, *S. yukonense* (*Semple & Semple 10624* WAT). **G.** Mature fruit. **H.** Fruit body. **I.** Silhouette of upper portion of pappus. **J.** Tips of primary whorl bristles. **K.** Tips of primary inner whorl bristles (lower magnification than D–F). **L.** Tip of secondary outer whorl bristle. **M.** Single secondary outer whorl bristle. **N.** Anthocyanotic barb of primary whorl bristle near base; diffuse pigment also present in shaft.

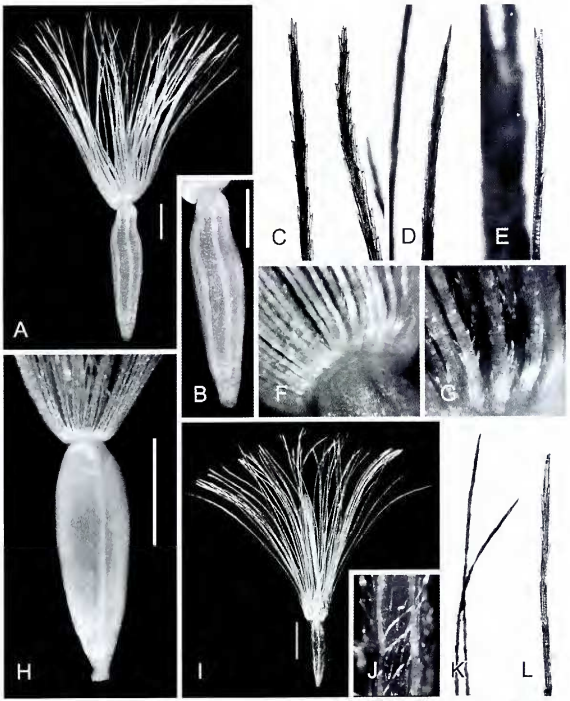

FIG. 4. Fruit traits in *Symphyotrichum* subg. *Symphyotrichum*, disc fruits I; scale bars = 1 mm. **A–F.** Sect./subsect. *Symphyotrichum*, *S. retroflexum* (*Semple & Chmielewski 6217* WAT). **A.** mature fruit. **B.** Fruit body detail. **C.** Tips of primary inner whorl bristles. **D.** Tip of primary outer whorl bristle. **E.** Tip of secondary outer whorl bristle. **F–G.** Base of pappus showing overlapping of bristles. **H.** Subsect. *Heterophylli*, *S. oolentangiense* (*Semple 2477* WAT) fruit body. **I–L.** Sect. *Conyzopsis*, *S. ciliatum* (*Houle & Legault 53* WAT). **I.** Mature fruit. **J.** Fruit body detail. **K.** Upper portion of primary whorl bristles. **K.** Tips of primary inner whorl bristles. **L.** Tip of primary inner whorl bristle show in **K.**

see, fine, secondary outer bristles. In all cases in *Symphyotrichum*, such bristles were clearly situated on the outer rim of the pappus. It seems likely that other species also rarely produce a bristle or two of the vestigial secondary outer whorl; finding such bristles was rather serendipitous. Documenting how frequently such rare bristles occur will take considerable time-consuming effort.

In other North American genera examined, species had either a quadruple or triple pappus, with both occurring within *Eucephalus*, *Doellingeria*, and *Ionactis* (Table 1). Historically, the short secondary outer whorl of bristles has been noted in all three genera, which were assumed to have a double pappus. The long inner "whorl" is in fact composed of usually three distinct whorls; a secondary inner whorl with tapering bristles 50–80% the length of the primary inner whorl; a primary outer whorl with tapering bristles 90–95% the length of the primary inner whorl; and a primary inner whorl of bristles with weakly to very strongly clavate bristles. Although species of *Doellingeria* have been treated as members of *Aster* sect. *Triplopappus*, their inner primary bristles are not as strongly clavate as those of some species of *Eucephalus*, which had not been reported to have two distinct whorls of longer inner bristles. These strongly clavate bristles were given a maximum score of 4 in Table 1, but they were more distinctly clavate than any *Solidago* and deserve a score of 5 on the 0–4 scale developed for goldenrods (Hood & Semple 2003).

The cypselae of at least some individuals of some species of *Eurybia* also have a quadruple pappus. Species in the related genus *Herrickia* also rarely had the short secondary outer whorl. The JCS laboratory is currently examining pappus traits in each of these $x = 9$ genera in detail and will report the results in a future paper.

Within the North American Clade some clades have lost one or more whorls of bristles, but not always the same whorl. In the Symphyotrichinae, the three longer whorls of bristles have generally been retained, but the short secondary outer whorl is absent or rarely vestigially present. In the Chrysopsidinae, the $x = 9$ genera have retained all four whorls to varying degrees, while the lower base number taxa have progressively lost the secondary inner and the secondary outer whorls (Semple, accepted). In the Solidagininae, some genera have retained the secondary outer whorl but lost the secondary inner whorl (e.g. *Sericocarpus*) while other genera have retained only the inner two primary whorls and usually lack the secondary outer whorl or possess it in a vestigial state (Hood & Semple 2003). Additional studies of all other subtribes and clades are needed to determine how many whorls of pappus bristles are really present. We note that several species that have been included in *Haplopappus* sensu Hall (1928) have been found to have either a double or triple pappus; this will be reported on in more detail in a future paper.

A few species of Eurasian and African asters were also examined to ascertain whether or not a quadruple pappus occurred in "Basal Group/Southern

Hemisphere Grade taxa" (Noyes & Rieseberg 1999) of Astereae. Four whorls were observed in species of *Aster* (one European, two eastern Asian species) and *Galatella* (Table 1); there were very few short outer bristles and only a few mid length bristles. In the *Crinitaria-Linosyris* group, which is more basal in the tribal phylogeny then *Aster* (Semple et al. 2002), the two species examined (Table 1) had numerous bristles that might be interpreted as four whorls or as a single series grading from very short outer bristles to long inner ones that were very weakly clavate. In both cases the pappus was different from that of North American basal genera. The pappus of the one species of *Felicia* examined lacked short and mid length bristles. The long bristles were slightly varied in length and some possibly were very narrowly clavate. The pappus was more like the most derived ones seen in some North American species, themselves known to be derived. The JCS laboratory has started a large systematic study of pappus variation in the Basal Grade genera of the Astereae and will report on the results in a future paper. At this point, however, it is clear that a quadruple pappus occurs in both the North American Clade and the some genera of Basal Grade of Astereae. A quadruple pappus is a plesiomorphic trait for the North American Clade; loss of whorls to three, two or one are derived states.

SYSTEMATICS IMPLICATIONS

Although *Symphyotrichum* has a triple pappus, for practical purposes, such as preparing keys to genera, it may be most convenient to treat the genus as having an "appearing simple" pappus (i.e., evidently having a single whorl of bristles), except possibly for sect. *Conyzopsis*, which has a distinctive pappus due to its numerous bristles in two similar whorls. In phylogenetic studies, the genus must be recognized as having a triple pappus with a vestigial fourth whorl in at least some species. The low number of secondary inner bristles and their apparent absence in some species reduces the value of this feature for purposes of identification. As well, for most species the low degree of clavateness of the primary inner bristles makes the condition not immediately obvious, as is clearly demonstrated by the fact that no one reported this before. Had we not begun with *Solidago*, we also might not have recognized the triple/quadruple pappus nature of the Symphyotrichinae genera of asters. In some cases, the triple nature of the pappus is only revealed by the small differences in average lengths of the three longer whorls. In Semple et al. (2002), the cypselae of 25 species of *Symphyotrichum* were illustrated in technical line drawing. Only a few of these can be interpreted now as showing differences in the lengths of the primary outer and inner whorl bristles, e.g. *S. praealtum* (Poir.) Nesom var. *praealtum*, and none illustrate the presence of the few-bristled shorter secondary inner whorl. Likewise, only three of the four whorls of pappus bristles of *Doellingeria umbellata* were illustrated; again the secondary inner whorl is missing. This is noted here to emphasize that differences between the secondary inner, the pri-

mary outer, and the inner pappus series in the North American Clade of the tribe Astereae are at times minor and difficult to see, but are nonetheless real.

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